Selective harvest of sooty shearwater chicks: effects on population dynamics and sustainability

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Running headline: Population effects of selective harvest

1 Summary

1. Selectivity of harvest influences harvest sustainability because individuals with different characteristics contribute differently to population growth. We investigate the effects of selection based on chick weight on a traditional harvest of the sooty shearwater (*Puffinus griseus)* by Rakiura Maori in New Zealand.

2. We develop a periodic stage-structured matrix population model and incorporate seasonal harvest of three weight classes of chicks. Intensity and selectivity of harvest are defined in terms of weight-specific hazard functions.

3. We investigate the effect of harvest intensity and selectivity on population growth rate, λ, and the chick exploitation rate, E. We also consider the interaction of chick harvest and adult mortality.

4. λ decreases and E increases as harvest intensity increases. At low harvest intensities, selection has little effect on λ. At high harvest intensities, λ increases as selectivity increases because of the nonlinear relationship between harvest intensity and the probability of being harvested.

5. λ is determined almost completely by E, irrespective of the combination of harvest selectivity and intensity producing E. This is true for both general patterns of selectivity and specific patterns estimated from empirical data.

6. The elasticities of λ, the net reproductive rate, and the generation time are unaffected by selectivity and show only small responses to harvest intensity.

7. Adult sooty shearwaters are killed as bycatch in long-line and driftnet fisheries. Such mortality of adults has an effect on λ about ten-fold greater than an equivalent level of chick harvest.

8. The sustainability of any combination of chick harvest and adult mortality depends on the resulting reduction in λ. We explore these results in relation to indices of sustainability, particularly the United States MMPA standards.

Keywords: matrix population models, demography, petrel, elasticity, traditional harvest.

2 Introduction

The sustainability of a harvest, i.e. whether harvest permits non-negative population growth, depends on the characteristics of the harvest, the organism's life history, and additional sources of mortality. Important characteristics of the harvest include the number, proportions, and type of individuals harvested, and the timing of the harvest within the year and within the life cycle (e.g. Olmstead and Alvarez-Buylla 1995; Jenson 2000; Frekleton et al. 2003). The life history of the organism determines how harvest affects the potential for population growth. Finally, harvest is rarely the sole source of human-imposed mortality, and the effects of harvest must be considered in the context of other such impacts (e.g., bycatch, pollution, or habitat destruction).

Selective harvest, in which individuals of different types are taken in proportions other than those in which they occur in the population, affects both the number and type of individuals harvested. Selection may result from harvester preferences, harvesting technology, behaviour of the harvested species, or management requirements, and may be intentional or unintentional. Selective harvest affects sustainability because different types of individuals contribute differently to population growth.

Selection on a gross scale, e.g., juvenile versus adult, is often imposed on managed harvests and accounted for in evaluating harvest impacts. Selection on less obvious characteristics, e.g., foraging ability or physiological condition, may be equally important. It is well-documented that apparently similar individuals can differ greatly in their reproductive contributions to future generations (e.g. Clutton-Brock 1988; Newton 1989). For example, less than one third of breeders and less than 10% of fledglings produce future recruits in some avian species (Coulson 1988; Wooller et al. 1988; Mills 1989; Newton 1989; Dann and Cullen 1990). In such cases, selectivity can have profound implications for sustainability. Yet such differences are less likely to be identified or measured, so are likely to be overlooked in evaluating harvest impacts.

Issues of sustainability and selectivity arise in the harvest of the sooty shearwater (*Puffinus griseus*) in New Zealand. The sooty shearwater is a medium-sized (650-1000g) procellariiforme. It is long-lived, has delayed maturity (first breeding at about 7 years) and low fecundity (lays at most one egg each breeding season). It is a colonial breeder, nesting in burrows, primarily on offshore islands. Sooty shearwaters are thought to number in the millions (Warham and Wilson 1982; Miskelly et al. 2001) but the species is listed as Near Threatened by the IUCN (Birdlife International 2004) because of population declines. Population declines have been indicated on both the wintering grounds (Veit, Pyle & McGowan 1996; Veit et al. 1997) and on the breeding grounds (Lyver, Moller & Thompson 1999; Lyver 2000a; Gaze 2000; Jones 2000; Scofield 2001; Scofield and Christie 2002).

By-catch of sooty shearwaters in ocean fisheries, particularly the central North Pacific driftnet fisheries, has also been a significant problem (Uhlmann 2003). More than 350,000 were taken annually from 1978–1990 (Ogi et al. 1993) and DeGange et al. (1993) suggest a worst case scenario of 1.2 million caught per year in the 1980s. High-seas driftnet fisheries were closed in 1993, but driftnet fishing persists in Russian and Mediterranean waters (Uhlman 2003) and current mortality levels are unknown.

The Rakiura Maori people of New Zealand conduct a traditional harvest of sooty shearwaters (tītī in the Maori language) on 36 islands around Stewart Island, the southernmost of New Zealand's three main islands (Department of Lands and Survey 1978; Wilson 1979; Robertson and Bell 1984, Anderson 1997). This harvest, generally referred to as muttonbirding, (Wilson 1979; Waitangi Tribunal 1991) is governed by the Tītī Regulations, which prohibit the harvest of adults, restrict access to the islands and the timing of the harvest and include provisions to protect the island habitat (e.g., measures to prevent predator introductions). The extent of the harvest is unknown

but may be as high as 250,000 birds annually (Warham 1996). The capacity for harvest has increased with new technology such as charter boat and helicopter transport, wax cleaning methods, and changes in the attendance of harvesters (Lyver 2000b). Maori culture places great importance on this harvest, and recent perceived changes in population status have led to concerns about its sustainability (e.g., Wilson 1979).

The harvest season (1 April to 31 May) is divided into two periods. The first period, the 'nanao' in the Maori language, starts on 1 April (Wilson 1979). During this period chicks are extracted from their burrows using a wire probe. The second period, the 'rama', begins when chicks start emerging from their burrows at night in preparation for fledging (usually about 20 April) allowing harvesters of pick them up off the ground. The harvest ends when chicks become scarce, usually around mid-May.

The harvest is selective: harvesters prefer heavier, more developed chicks (Lyver 2000a; Hunter, Moller & Kitson 2000b). We investigate the impacts of this selectivity on population growth, and how those impacts interact with fisheries by-catch of adults. We apply out model to patterns of selectivity estimated on a harvested island (Putauhinu), and discuss the problems involved in determining levels of harvest compatible with sustainability.

3 A demographic model for the sooty shearwater

3.1 Model structure

To account for the restriction of harvest to chicks during a specific period of the year we used a periodic stage-structured matrix model (Caswell and Trevisan 1994; Caswell 2001, Section 13.1). We divided the year into 3 periods: (1) from the beginning of the nanao to the beginning of the rama; (2) from the beginning of the rama to fledging; and (3) from fledging to the beginning of the next nanao. We refer to these periods as the nanao, rama and non-harvest periods, respectively. In each period, we classified individuals into seven stages: 1) light chicks, 2) medium chicks, 3) heavy chicks, 4) first-year pre-breeders, 5) second-year pre-breeders, 6) third-year pre-breeders and 7) breeders (Fig. 9). This is the model structure used by Hunter, Moller & Fletcher (2000a), but with the year divided into seasons and chicks divided into three weight classes.

We classified chicks into weight classes because survival and probability of return to the colony are related to chick weight at fledging in the sooty shearwater (Sagar and Horning 1997; Scofield 2001) and in other procellariiformes (e.g. Perrins 1966), and in some species heavier chicks have higher eventual reproduction (Lindstrom 1999, Cam, Monnat & Hines 2003). We defined three weight classes (500–700g, 700–900g and $\geq$ 900g), which we will refer to as small, medium and large chicks. Chicks less than 500g were excluded from all analyses. These chicks are poorly developed, lethargic, and unlikely to survive (Sagar and Horning 1997), and so do not contribute to population demography. They are also rejected by harvesters.

The life cycle graph in Fig. 9 shows the transitions among, and reproductive contributions of, the seven stages for the three periods in the annual cycle (cf. Caswell 2001, Sec. 13.2). We denote the projection matrices for the nanao, rama and non-harvest periods as $\mathbf{B}$, $\mathbf{C}$ and $\mathbf{D}$ respectively (Fig. 9). We begin by describing these matrices in the absence of harvest. Where necessary, we use superscripts to denote the period of the year; e.g., $P_7^{(2)}$ is the survival probability of stage 7 (breeders) during period 2 (the rama).

3.1.1 Nanao and rama periods - matrices B and C

Chicks may increase or decrease in weight during the nanao and rama, depending on the amount of food received and their activity level, so all transitions among the three weight classes are possible (Fig. 9). These two periods are short (3–3$\frac{1}{2}$ weeks) relative to the annual cycle, so pre-breeders and breeders remain in their respective stages. The matrix **B** for the nanao period is

$$\mathbf{B} = \left(\begin{array}{ccc|ccc|c} G_{11}^{(1)} & G_{12}^{(1)} & G_{13}^{(1)} & 0 & 0 & 0 & 0 \\ G_{21}^{(1)} & G_{22}^{(1)} & G_{23}^{(1)} & 0 & 0 & 0 & 0 \\ G_{31}^{(1)} & G_{32}^{(1)} & G_{33}^{(1)} & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & P_4^{(1)} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_5^{(1)} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & P_6^{(1)} & 0 \\ \hline 0 & 0 & 0 & 0 & 0 & 0 & P_7^{(1)} \end{array}\right) \qquad \text{eqn 1}$$

The matrix **C** for the rama is the same, with the superscript 1 (denoting the nanao harvest period) replaced by 2 (denoting the rama harvest period) . In these matrices,

$$P_i^{(k)} = s_i^{(k)} \qquad i = 4, \ldots, 7 \qquad \text{eqn 2}$$

$$G_{ij}^{(k)} = w_{ij}^{(k)} \qquad i, j = 1, 2, 3 \qquad \text{eqn 3}$$

where $s_i^{(k)}$ is the probability an individual in stage i survives through period k, and $w_{ij}^{(k)}$ is the probability a chick moves from weight class j to weight class i during period k. In the absence of harvest, chick mortality is negligible during these periods (less than 1%), so we set chick survival to 1.0.

3.1.2 Non-harvest period - matrix D

The matrix **D**, describing the non-harvest period, includes transitions of chicks to the pre-breeder stage, transitions of pre-breeders to the next pre-breeding stage or to the breeding stage, and reproduction by individuals that make the transition to the breeder stage (Fig. 9):

$$\mathbf{D} = \left(\begin{array}{ccc|ccc|c} 0 & 0 & 0 & 0 & F_{15}^{(3)} & F_{16}^{(3)} & F_{17}^{(3)} \\ 0 & 0 & 0 & 0 & F_{25}^{(3)} & F_{26}^{(3)} & F_{27}^{(3)} \\ 0 & 0 & 0 & 0 & F_{35}^{(3)} & F_{36}^{(3)} & F_{37}^{(3)} \\ \hline S_1^{(3)} & S_2^{(3)} & S_3^{(3)} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4^{(3)} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5^{(3)} & P_6^{(3)} & 0 \\ \hline 0 & 0 & 0 & 0 & P_5^{(3)} & G_6^{(3)} & P_7^{(3)} \end{array}\right) \qquad \text{eqn 4}$$

The survival probabilities, S_i, of chicks to the first pre-breeder stage are

$$S_i^{(3)} = s_0 r_i \qquad \text{eqn 5}$$

where s_0 is the survival of medium chicks through the non-harvest period, and r_i scales survival of small and large chicks relative to that of medium chicks.

The pre-breeder and breeder transitions, G_i and P_i, and the fertilities, F_{ij}, depend on survival, immigration, emigration, the probability of breeding and breeding success (see Hunter et al. 2000a

for details). We assumed a post-breeding birth pulse model, so pre-breeders that become breeders during the year contribute to reproduction, and adult survival appears in the fertilities. Each reproductive stage that contributes to the fertilities (stages 5–7) produces small, medium, and large chicks in the same proportions.

$$
\begin{aligned}
G_4^{(3)} &= s_4^{(k)} && \text{eqn 6}\\
G_5^{(3)} &= s_5^{(k)}\,(1+m)\,(1-\gamma) && \text{eqn 7}\\
G_6^{(3)} &= s_6^{(k)}\,(1-u)\,\gamma && \text{eqn 8}\\
P_5^{(3)} &= s_5^{(k)}\,(1+m)\,\gamma && \text{eqn 9}\\
P_6^{(3)} &= s_6^{(k)}\,(1-u)\,(1-\gamma) && \text{eqn 10}\\
P_7^{(3)} &= s_7^{(k)} && \text{eqn 11}\\
F_{i5}^{(3)} &= s_5^{(3)}\,(1+m)\,\gamma\,b\,q_i && \text{eqn 12}\\
F_{i6}^{(3)} &= s_6^{(3)}\,(1-u)\,\gamma\,b\,q_i \qquad i=1,2,3 && \text{eqn 13}\\
F_{i7}^{(3)} &= s_7^{(3)}\,(1-g)\,b\,q_i && \text{eqn 14}
\end{aligned}
$$

Here m is the immigration rate of pre-breeders of age 3, u is the emigration rate of pre-breeders during the non-harvest period, γ is the probability of breeding for the first time, b is the probability of breeding success, q_i is the probability that new chick is in weight class i, and g is the probability that a breeder skips breeding.

3.1.3 The annual cycle

Dynamics for the annual cycle (Fig. 9) are described by multiplying **B**, **C**, and **D** in order to form an annual population projection matrix **A**. Starting at period 1, 2 or 3 this gives $\mathbf{A}^{(1)} = \mathbf{DCB}$, $\mathbf{A}^{(2)} = \mathbf{BDC}$ or $\mathbf{A}^{(3)} = \mathbf{CBD}$, respectively, where the superscript on **A** denotes the period at which the projection starts. The long-term annual growth rate of the population is given by the largest eigenvalue, λ, of any of the $\mathbf{A}^{(k)}$.

The stable stage distribution and reproductive value distribution at period k are given by the right and left eigenvectors $\mathbf{w}^{(k)}$ and $\mathbf{v}^{(k)}$ of $\mathbf{A}^{(k)}$ corresponding to λ. The eigenvectors depend on the period at which the population is observed, so population structure and reproductive value cycle seasonally with period three.

3.2 Modelling harvest and selection

Harvest reduces the transition probabilities among chick weight classes during the nanao and the rama. Let H_j denote the event that a chick in weight class j is harvested. The transition probability $G_{ij}^{(k)}$ (in equation eqn 3, dropping the superscripts for clarity) becomes

$$G_{ij} = w_{ij}\,(1 - P[H_j]) \qquad \text{eqn 15}$$

We write the harvest probabilities in terms of instantaneous *harvest rates* or *hazard functions*, h_j, so the probability of harvest in a short time interval δt is $h\delta t$; Cox & Oakes (1985). The probability of harvest is

$$P[H_j] = 1 - e^{-h_j} \qquad \text{eqn 16}$$

using the length of the period as the unit of time (Fig. 9).

3.3 Parameter estimation

Data on chick growth and harvest were collected on Putauhinu Island, a 148 ha island located off the southwest coast of Rakiura, during the 1998 and 1999 harvest seasons. We measured the mass of harvested chicks and of chicks available for harvest at regular intervals (see Hunter et al. 2000b for details). These data were used to estimate transitions among chick weight classes, the size distributions of harvested and of available chicks, and the probability of a breeder producing a chick in a given weight class (Tables 1-3).

Published data on sooty shearwaters and the closely related short-tailed shearwater (*Puffinus tenuirostris*), were used to estimate all other parameters in the model (Bradley, Skira & Wooller 1991, Sagar and Horning 1997; Tables 1 & 2). Details on estimation of these parameters are given in Hunter et al. (2000a).

3.3.1 Chick growth $\left(w_{ij}^{(k)}\right)$ and relative survival r_i

Transition probabilities in the absence of harvest were estimated from four sites on Putauhinu Island in 1998 and 1999 (for details of methodology see Hunter et al. 2000b). Transition probabilities during the nanao, $w_{ij}^{(1)}$, were estimated as the proportion of chicks in weight class j during the first six days of the nanao that were in weight class i during the first six days of the rama (Table 1). Transition probabilities for the rama, $w_{ij}^{(2)}$, were estimated as the proportion of chicks in weight class j during the first six days of the rama that were in weight class i on the last date weighed after 6 May. Weighted averages and multinomial standard errors were calculated for the combined 1998 and 1999 data (Table 1).

Survival of small, medium, and large chicks through the non-harvest period was estimated from recapture data on 500 chicks banded on The Snares in 1972 (Sagar and Horning 1997; Scofield subm). The annual survival rate for each weight class was estimated as the proportion of chicks in that class that were recaptured, raised to the power of the reciprocal of the average number of years from banding to recapture. The adjustment factor r_i in (eqn 5) was the annual survival rate of weight class i relative to that of medium chicks (weight class 2; Table 2). Standard errors for the r_i were calculated using the delta method (Kendall and Stuart 1979).

The probability of a breeder producing a chick in weight class j, q_j, was estimated as the proportion of chicks in weight class j during the first six days of the nanao.

The probability of breeding for the first time, γ, is the probability of transition from pre-breeder to breeder, conditional on survival. It was calculated from the mean, $\bar{T}$, and variance, $V(T)$ of the pre-breeder stage duration (equation 6.114 of Caswell 2001). The mean stage duration was estimated as the mean age of first breeding minus the age of entry into the pre-breeding stage.

4 Analysis and Results

4.1 Population growth rate

We used a Monte Carlo approach to generate the standard error of λ. We drew each parameter from a normal distribution (except m which was drawn from a uniform distribution; see Hunter et al. 2000a), constructed the matrices $\mathbf{B}$, $\mathbf{C}$, $\mathbf{D}$, and $\mathbf{A}$, and calculated λ for each $\mathbf{A}$ matrix for 100,000 replicates. The distribution of the resulting estimates of λ describe the uncertainty arising from uncertainty in the parameters.

In the absence of harvest, $\lambda = 0.985$, with standard error of 0.033 and 95% confidence interval 0.953–1.02. We use this value as a baseline against which to measure the effects of harvest rather

than focusing on the value itself.

4.2 Harvest intensity and selectivity

4.2.1 Describing harvest intensity and selectivity

We defined the harvest intensity for a given period as the sum of the instantaneous stage-specific harvest rates; $h_{\text{tot}} = \sum_j h_j$. We defined selectivity in terms of the relative values of the h_j. Denoting the harvest rates for small, medium, and large chicks as h_S, h_M, and h_L, we defined selectivity as

$$\Delta = \frac{h_L}{h_S}. \qquad \text{eqn 17}$$

On this proportional scale, $\Delta = 2$ implies that the harvest rate on large chicks is twice that on small chicks; $\Delta = 1/2$ implies the same selectivity, but in the opposite direction.

We explored three simple models for selection, which differed in the value of h_M relative to h_L and h_S.

- **Model 1.** The harvest rate for medium chicks is intermediate, on a proportional scale, between h_S and h_L; i.e., $\frac{h_M}{h_S} = \frac{h_L}{h_M} = \sqrt{\Delta}$
- **Model 2.** There is no selection between small and medium chicks, so that $h_S = h_M$.
- **Model 3.** There is no selection between medium and large chicks, so that $h_M = h_L$.

Any harvesting regime results in an exploitation rate, defined as the proportion of chicks harvested, which depends on the stage-specific harvest rates and the size composition of the chick population. Let p_j be the proportion of chicks in weight class j; the exploitation rate for a given period is

$$\begin{aligned} E &= \sum_j p_j P[H_j] \\ &= \sum_j p_j \left(1 - e^{-h_j}\right) \end{aligned} \qquad \text{eqn 18}$$

When harvest occurs in both periods, the overall exploitation rate is calculated from the proportions harvested in the two periods as

$$E = 1 - (1 - E_n)(1 - E_r), \qquad \text{eqn 19}$$

where E_n and E_r are the exploitation rates during the nanao and rama, respectively.

4.2.2 Effects on population growth

To describe the impact of harvest, we varied h_{tot} and Δ over a wide range of values, for each selection model in each harvest period separately. We computed λ and E over those ranges. Fig. 9 shows the results for harvest during the nanao; results for harvest during the rama are very similar and not shown here.

Not surprisingly, increasing harvest intensity increases E and reduces λ (Fig. 9). The effect of selectivity depends on harvest intensity. At low intensities, selection has little effect, as shown by the nearly vertical contours of λ and E. At high intensities, λ increases as selection for large or small chicks becomes extreme. This occurs because the relationship between harvest intensity and

the probability of being harvested in equation (eqn 16) is nonlinear. When harvest intensity for a given stage is very high, nearly every individual in that stage is taken. Suppose that selection shifts towards large and away from small chicks. The probability of taking small chicks declines, but once the probability of taking large chicks asymptotes it cannot increase further. This has the effect of reducing E and increasing λ. Thus, in the limit as both intensity and selection become large, harvest takes all of the selected stage(s) and none of the other(s).

The details of this response, and how quickly λ and E respond to Δ and h_{tot}, depend on the selection model and on the stable stage distribution of chicks. For example, without harvest, the stable stage distribution at the beginning of the nanao has approximately 12%, 42% and 46% small, medium, and large chicks, respectively. Under Model 2, selection for small and medium chicks is the same, so selection for either small (and therefore also medium) or large chicks affects about 50% of the chick population. This results in an approximately symmetrical response of λ to changes in selectivity (Fig. 9c,d). Under Model 3, selection for medium and large chicks is the same. Increasing Δ selects for large and medium chicks and against small chicks. Since small chicks make up only 12% of the population, protecting them has little effect on λ. Conversely, decreasing Δ selects against medium and large chicks, which make up 88% of the population, producing a large impact on λ (Fig. 9e,f).

These patterns are insensitive to r_i, w_{ij}, and q_i, because changes in these parameters have little effect on the stable stage distribution. This suggests that selectivity is insensitive to differences in survival among the chick weight classes. The response patterns are also very similar between the two harvest periods most likely because the stable stage distributions in the two periods are similar.

The responses of λ and E are strongly negatively correlated (Fig. 9). The effects of harvest intensity and selectivity on λ depend almost entirely on effects on E. Thus, to a good approximation, λ can be treated as a function of exploitation rate alone, independent of the combination of harvest rate and selectivity that produced that exploitation rate. The function is nearly linear when E is small, with an increase in E of 1 percentage point causing a decrease in λ of about 0.06 percentage points.

4.2.3 Effects on elasticities, R_0, and generation time

In addition to its effects on λ, harvest also affects the sensitivity and elasticity of λ to the demographic parameters. Because elasticities are sometimes used to evaluate management plans, it is important to know if their qualitative patterns are likely to change due to harvest.

The elasticity of λ to a parameter θ is

$$e_\theta = \frac{\theta}{\lambda}\frac{\partial \lambda}{\partial \theta} \qquad \text{eqn 20}$$

and $\partial\lambda/\partial\theta$ in (eqn 20) depends on how θ affects the seasonal matrices **B**, **C**, and **D**:

$$\frac{\partial \lambda}{\partial \theta} = \sum_{i,j} \frac{\partial \lambda}{\partial b_{ij}}\frac{\partial b_{ij}}{\partial \theta} + \sum_{i,j} \frac{\partial \lambda}{\partial c_{ij}}\frac{\partial c_{ij}}{\partial \theta} + \sum_{i,j} \frac{\partial \lambda}{\partial d_{ij}}\frac{\partial d_{ij}}{\partial \theta} \qquad \text{eqn 21}$$

The sensitivities of λ to b_{ij}, c_{ij}, and d_{ij} in (eqn 21) were calculated according to equation (13.40) of Caswell (2001).

In the absence of harvest, the elasticities of λ are highest to breeder survival ($e_{s_7} = 0.73$), stage duration ($e_d = -0.39$), and survival of third-year pre-breeders ($e_{s_6} = 0.18$). The pattern of elasticities is very robust to changes in the intensity of harvest (Fig. 9). Results are similar over a wide range of selectivity levels ($0.01 \leq \Delta \leq 100$).

The net reproductive rate, R_0, and the generation time, τ, can be calculated by decomposing a projection matrix into two components, one representing transitions of existing individuals and the other the production of new individuals (Caswell 2001). We applied the calculation to the seasonal matrices (Appendix A). Net reproductive rate declined from 0.79 with no harvest to 0.42 for $h_{\text{tot}} = 2$. Generation time increased from 15.4 with no harvest to 18.5 for $h_{\text{tot}} = 2$. Changes in τ are important in cases where conservation status is expressed in terms of changes over generations (e.g., IUCN 2001). In this case, however, even intense harvest ($h_{\text{tot}} = 2$) only causes a 20 % change in τ.

4.3 The harvest on Putauhinu Island

We turn now to data on the harvest on Putauhinu Island. We first estimate the pattern of selectivity exhibited by the harvesters on Putauhinu Island, and then explore the implications of that selectivity on λ and E.

4.3.1 Estimating selectivity on Putauhinu

The data available are the size composition of the population (p_i = proportion of the chicks in weight class i) and of the harvest (f_i = proportion of harvested chicks in weight class i). For each period, we want to calculate the harvest rates, h_i, that satisfy (eqn 16). Using Bayes' Theorem, it can be shown that

$$f_i = \frac{\left(1 - e^{-h_i}\right) p_i}{\sum_{j=1}^{3} \left(1 - e^{-h_j}\right) p_j} \qquad i = 1, 2, 3 \qquad \text{eqn 22}$$

In addition, the exploitation rate E for that period must satisfy

$$E = \sum_{j} \left(1 - e^{-h_j}\right) p_j \qquad \text{eqn 23}$$

Equation (eqn 22) is a linear system of equations in e^{-h_i}, but it is rank deficient and so only provides *relative* values of the h_i. It can be solved for *absolute* values only with the an additional constraint, which can be provided by specifying the value of E in (eqn 23). For small values of E, the h_i converge to constant relative values. In our case, those relative values remain nearly constant for $0 \leq E \leq 0.25$. The exploitation rate on Putauhinu Island is about 5%. Thus, the relative harvest rates obtained from (eqn 22) and (eqn 23) are good estimates.

The resuls show that during the nanao harvesters select for large chicks and against medium and small chicks (Table 4. During the rama there was selection for medium chicks and against small and large chicks. The two patterns in sequence result in selection for medium and large chicks and against small chicks, but the degree of selectivity is somewhat lessened.

4.3.2 Effects of harvest intensity and selectivity on Putauhinu Island

To explore the effect of the Putauhinu selectivity pattern on λ and E, we fixed the selection pattern at the estimated values of h_i and varied h_{tot} (Fig. 9). Increased harvest intensity decreased λ and increased E. Results for 1988 and 1999 were nearly identical. As for our idealized selection models, there was a very tight relationship between λ and E (Fig. 9). Over the range of exploitation rates considered reasonable for Putauhinu Island ($0 \leq E \leq 0.1$), an increase in E of one percentage point would reduce λ by 0.06 percentage points.

4.4 Effects of adult bycatch

Only the chicks of sooty shearwaters are harvested, but sensitivity analyses of long-lived species show that mortality of adults has a greater effect on population growth rate than mortality of chicks (e.g., Russell 1999; Hunter 2000a; Heppell, Caswell & Crowder 2000). Therefore adult mortality due to bycatch could be expected to reduce population growth and affect the sustainable level of chick harvest.

To evaluate this effect, we added extra mortality to stage 7 (adults that had bred at least once) to mimic the effects of bycatch. This is conservative because we did not add mortality to pre-breeders although they are probably also subject to bycatch. We assumed that bycatch occurred during the non-harvest period and that it was not selective. We described it in terms of a hazard rate h_7, assuming that bycatch and other sources of mortality were independent. Adult survival during the non-harvest period thus became

$$P_7^{(3)} = s_7^{(3)}\ e^{-13.9 h_7} \qquad \text{eqn 24}$$

where h_7 is multiplied by a 13.9 to adjust for the difference in the length of the harvest and non-harvest periods (cf equation (eqn 14)). The proportion of breeders dying from bycatch is $1 - e^{-13.9\,h_7}$, which we term adult exploitation.

As expected, adult mortality has a much greater impact on population growth rate than does chick harvest (Fig. 9). With no selection, a 5% chick exploitation rate reduces λ by only 0.3 percentage points, whereas a 5% adult exploitation rate reduces λ by 3 percentage points (Fig. **??**). Combining chick harvest and adult bycatch reveals combinations of chick and adult exploitation that would be sustainable, as a function of the reduction in λ that can be tolerated (Fig. 9). For example, if the population could withstand a 2 percentage point reduction in λ, a 5% exploitation of chicks would be sustainable only if adult exploitation was less than $\approx$ 2%. Small changes in adult survival or exploitation have a large impact on λ; estimates of uncertainty associated with these measures will therefore be very important to quantitative evaluations of sustainability.

5 Discussion

5.1 Impacts of selective harvest

Population growth rate is a particularly powerful index for evaluating harvest effects because it measures the ability of a population to increase when subjected to any specified level of exploitation. Other authors have used demographic models to study harvest (e.g., Getz and Haight 1989; Olmsted and Alvarez-Buylla 1995; Frederiksen, Lebreton & Bregnballe 2001; Freckleton et al. 2003; Marboutin et al. 2003), but the effect of selectivity of harvest within life cycle stages has received relatively little attention.

Selectivity of the harvest on Putauhinu Island translates into large differences in harvest rates among weight classes. During the nanao, the harvest rate of large chicks was more than 5 times that of small chicks. During the rama, the harvest rate of medium chicks was greater than that of small or large chicks (Table 4). This is consistent with previous studies of selectivity of the harvest (Lyver 2000a; Hunter et al. 2000b).

Selectivity has little impact on λ unless the harvest is very intense. The population effects of removing an individual depends on quality (i.e., future contributions to reproduction) and on the contribution of it's stage to demography. The effect of quality differences among chick classes in our model is small because chicks move among classes during the nanao and rama (the w_{ij}; Table 1). The contribution of chick survival to population growth is small, and regardless of initial weight

all chicks become identical pre-breeders at the end of the first year (Fig. 9). Unpublished analyses suggest that selectivity would have greater impact on λ if differences among chicks were maintained to adulthood. There is evidence for such links between characteristics of young individuals and life history traits of adults in many taxa (e.g. Hales and Barker 2001; Metcalfe and Monaghan 2001; Lummaa and Clutton-Brock 2002). This warrants further investigation in the sooty shearwater and should be an important consideration for modelling selective mortality in other species.

Selective harvest can also have evolutionary effects if the traits involved are heritable (Ratner and Lande 2001); such effects have been shown in trophy hunting of large ungulates (Harris, Wall & Allendorf 2002; Coltman et al. 2003) and commercial harvest of fish stocks (Rowell, Stokes & Law 1989; Palumbi 2001; Conover & Munch 2002). This also warrants further investigation for the sooty shearwater and other seabird populations.

Our results are consistent with elasticity analysis. Harvest of chicks reduces fertility, whereas, like most long-lived species, population growth rate is much more elastic to changes in adult survival than reproduction (e.g., Hunter et al. 2000a). Because the elasticity analysis is robust to changes in h and Δ, our conclusions are likely to apply to populations over a range of conditions. They are also pertinent to populations experiencing other types of selective mortality, such as condition or size-dependent predation (e.g., ref) or weather related mortality.

5.2 Adult bycatch and sustainability of the harvest

Milner-Guland and Akçakaya (2001) reviewed five algorithms used to determine sustainable exploitation levels of harvested wild animals. The calculations depend on assumptions about population dynamics and on the desired safety margin, but each compares the exploitation rate to some function of the potential population growth rate.

The algorithm used under the US Marine Mammal Protection Act (MMPA; 16 U.S.C. 1361 et. seq.) is typical, and performed best, particularly under conditions of bias or uncertainty (Milner-Guland and Akçakaya 2001). The MMPA algorithm compares the number of animals killed by human activities with the "Potential Biological Removal" (PBR). The PBR is the product of 3 factors: one half the potential rate of increase, $R_{\max}$; a minimum estimate of population size, $N_{\min}$; and a "recovery factor" f that ranges between 0.1 and 1 (Wade 1998; Taylor et al. 2000).

$$PBR = \frac{1}{2} R_{\max} N_{\min} f \qquad \text{eqn 25}$$

The potential rate of increase is $R_{\max} = \lambda_{\max} - 1$, where $\lambda_{\max}$ is the maximum possible growth rate in the current environment, including all other sources of mortality but at low densities (to account for possible density-dependence). The minimum population size estimate is defined as the 20th percentile of the sampling distribution of the population estimate, which is assumed to be lognormal (Wade 1998). The recovery factor adjusts the conservatism of the standard. If the stock is classified as threatened or endangered, $f = 0.1$. Otherwise, f is larger the higher the quality of the data. This calculation is precautionary because both the use of a minimum population size estimate and f reduce the number of individuals that can be removed. If human-caused mortality exceeds the PBR, a series of management actions are triggered to reduce mortality.

This criterion compares a mortality rate with a potential population growth rate, requiring that

$$\frac{\text{removals}}{N_{\min}} \leq \frac{1}{2}(\lambda_{\max} - 1)\, f. \qquad \text{eqn 26}$$

The ratio of removals to $N_{\min}$ is a maximum estimate of mortality due to the removals. The models underlying the MMPA ignore population structure, treating all individuals as identical

(Wade 1998). In a structured population the effect of exploitation depends on which stages are targeted. In that case it is useful to phrase sustainability in terms of the reduction in λ, which integrates the effects of removal of different types of individuals into a single metric. We can use an algorithm analagous to the MMPA algorithm by expressing allowable removal (the left-hand side of Eq. (eqn 26)) as reduction in population growth rate.

Applied to sooty shearwaters, this approach would require that harvest, together with other human-caused mortality, not reduce λ by more than $0.5fR_{\max}$. We do not know $\lambda_{\max}$, but the MMPA uses a default value of 1.04 for cetaceans in the absence of data. The life-history of the sooty shearwater falls within the range of life-expectancy, fecundity and age at first breeding of cetaceans. Using $\lambda_{max} = 1.04$ and $f = 1.0$, an MMPA calculation would limit the reduction in λ to 2 percentage points. If we set $f = 0.5$ (because the data are fragmentary and the population may be declining) then λ could not be reduced by more than 1 percentage point.

Figure 9 shows the reduction in λ as a function of chick harvest and adult bycatch (the baseline value of λ has a negligible effect on these results). If the allowable reduction in λ is 2 percentage points, then the chick harvest on Putauhinu would meet the criterion provided adult exploitation was less than 2%. The harvest on other islands may not, such as Poutama, where the chick harvest rate is 20% (Lyver 2000a). With a more precautionary choice of $f = 0.5$, the harvest on Putauhinu would be sustainable only if adult exploitation was less than 1%.

We cannot say whether the sooty shearwater harvest is sustainable. We can, however, specify the information needed to make such an evaluation: a criterion of sustainability, estimates of the chick exploitation rate and adult mortality, and the level of uncertainty associated with each. These will not be easy to obtain, but each plays a critical role in evaluation of harvest impacts.

The Maori harvest is restricted to a few weeks of the sooty shearwater's life, on a few small islands. Its sustainability, however, can be evaluated only in the context of the complete life cycle and the geographical range of the population. Since the sooty shearwater can live for 40 years and migrates over a significant fraction of the globe, this will require connecting processes that operate at very small spatial and temporal scales with processes that operate at large spatial and temporal scales. In this, the tītī and the traditional Maori concerns for its preservation are a model for the problems facing many long-lived wide-ranging species and the people who want to understand and to preserve them.

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7 Appendix A

Net reproductive rate and generation time can be calculated by decomposing the projection matrix $\mathbf{A}$ into a matrix, $\mathbf{T}$, of transitions and a matrix, $\mathbf{F}$, of fertilities (Caswell 2001, Chapter 5). When fertility terms appear in only one matrix in a periodic product, this can be achieved by decomposing that matrix ($\mathbf{D}$ in our case) into a matrix of transitions, $\mathbf{T_D}$, and a matrix of fertilities, $\mathbf{F_D}$, and then writing $\mathbf{A} = \mathbf{BC}\left(\mathbf{T_D} + \mathbf{F_D}\right)$. This is equivalent to $\mathbf{A} = \mathbf{T} + \mathbf{F}$ with $\mathbf{T} = \mathbf{BCT_D}$ and $\mathbf{F} = \mathbf{BCF_D}$. From this decomposition we calculated the net reproductive rate, R_0, as the dominant eigenvalue of the matrix $\mathbf{R} = \mathbf{F}\left(\mathbf{I} - \mathbf{T}\right)^{-1}$ (Caswell 2001). We defined the generation time, τ, as the time required for the population to increase by a factor of R_0, thus $\tau = \log R_0 / \log \lambda$.

8 Tables

Table 1: Probability of making a transition from stage j to stage i (w_{ij}) and of survival in stage i (s_i) in the nanao and rama periods.

	Nanao		Rama	
Parameter	Estimate	SE	Estimate	SE
w_{11}	0.235	0.103	1.000	≤ 0.001
w_{21}	0.588	0.119	0.000	0.000
w_{31}	0.176	0.092	0.000	0.000
w_{12}	0.170	0.040	0.764	0.057
w_{22}	0.432	0.053	0.236	0.057
w_{32}	0.398	0.052	0.000	0.000
w_{13}	0.039	0.022	0.095	0.030
w_{23}	0.308	0.052	0.758	0.044
w_{33}	0.654	0.054	0.147	0.036
s_4	0.992	0.001	0.990	0.001
s_5	0.996	0.001	0.995	0.001
s_6	0.995	≤ 0.001	0.994	≤ 0.001
s_7	0.995	≤ 0.001	0.994	≤ 0.001

Table 2: Parameter estimates for the non-harvest period: q and r estimated for the sooty shearwater, all other parameter estimates taken from Hunter et al. (2000a).

Parameter		Estimate	SE
survival to 1-yr	s_0	0.583	0.024
1st year pre-breeder survival	s_4	0.882	0.011
2nd year pre-breeder survival	s_5	0.932	0.007
$\geq$ 3rd year pre-breeder survival	s_6	0.922	0.005
breeder survival	s_7	0.922	0.005
small chick survival adjustment	r_1	0.888	0.308
medium chick survival adjustment	r_2	1.000	0.124
large chick survival adjustment	r_3	1.030	0.120
proportion small chicks produced	q_1	0.121	0.023
proportion medium chicks produced	q_2	0.464	0.035
proportion large chicks produced	q_3	0.416	0.034
emigration	u	0.246	0.057
immigration	m	1.220	(0.439-1.174)*
breeding success	b	0.306	0.005
probability of skipping breeding	g	0.314	0.007
pre-breeder stage duration	$\bar{T}$	4.116	0.107
pre-breeder stage duration variance	$V(T)$	2.347	0.235

* This is the range, a standard error was not available

Table 3: Proportion of harvested chicks in weight stage z, $P(z|H)$, and proportion of chicks available for harvest in weight stage z, $P(z)$, on Putauhinu Island.

		1998		1999	
	stage (z)	Estimate	SE	Estimate	SE
			$P(z\|H)$		
nanao	1	0.000	0.014	0.029	0.007
	2	0.170	0.023	0.284	0.020
	3	0.830	0.023	0.688	0.020
rama	1	0.168	0.011	0.123	0.007
	2	0.613	0.015	0.592	0.011
	3	0.219	0.013	0.285	0.010
			$P(z)$		
nanao	1	0.115	0.036	0.124	0.029
	2	0.487	0.057	0.450	0.044
	3	0.397	0.055	0.426	0.044
rama	1	0.169	0.030	0.114	0.026
	2	0.494	0.040	0.315	0.038
	3	0.338	0.038	0.570	0.041

Table 4: Relative values of the instantaneous harvest rates, h_j, for small, medium and large chicks (scaled so $h_L = 1$) for the nanao and rama periods on Putauhinu Island.

	Nanao		Rama	
	1998	1999	1998	1999
small	0.00	0.14	1.54	2.15
medium	0.17	0.39	1.92	3.77
large	1.00	1.00	1.00	1.00

9 Figure captions

Figure 1 A seasonal life cycle graph for the sooty shearwater. Stages: 1 = small chicks, 2 = medium chicks, 3 = large chicks, 4 = 1st year pre-breeders, 5 = 2nd year pre-breeders, 6 = $\geq$ third year pre-breeders, and 7 = breeders. Matrices **B**, **C** and **D** describe transitions during the nanao, rama and non-harvest periods, respectively.

Figure 2 Probability of harvest, $P(H)$, as a function of the instantaneous harvest rate, h.

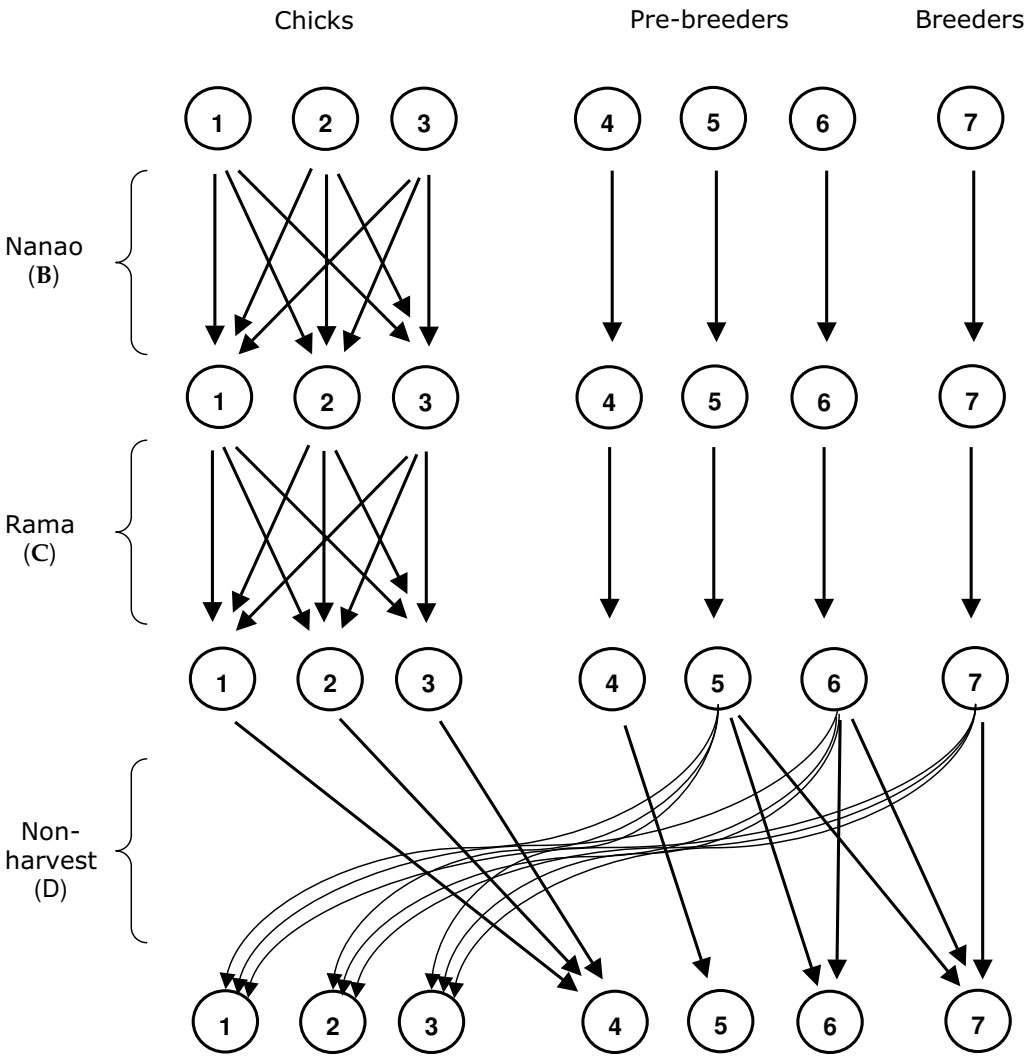
Figure 3 λ and E as a function of harvest intensity, h_{tot}, and the log of selectivity, $\log_{10}(\Delta)$, for each of three selection models: (a,b) Model 1, (c,d) Model 2, and (e,f) Model 3. Harvest occurs only in the nanao period.

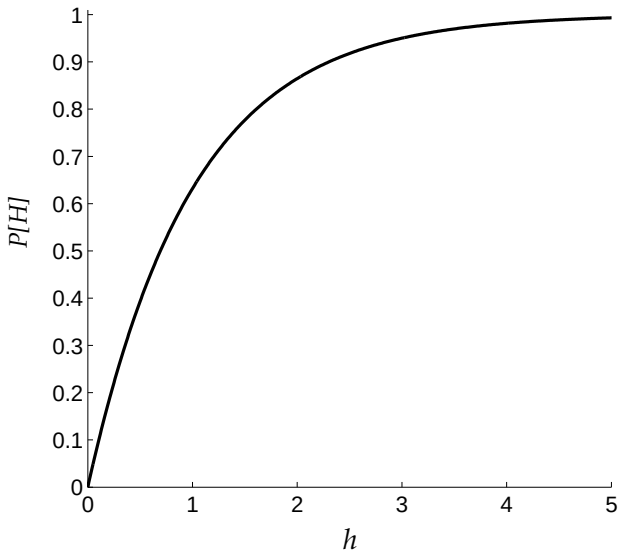
Figure 4 Corresponding values of λ and E for the entire range of values of harvest intensity, h_{tot} and log of selectivity, $\log_{10}(\Delta)$ shown in Figure 9.

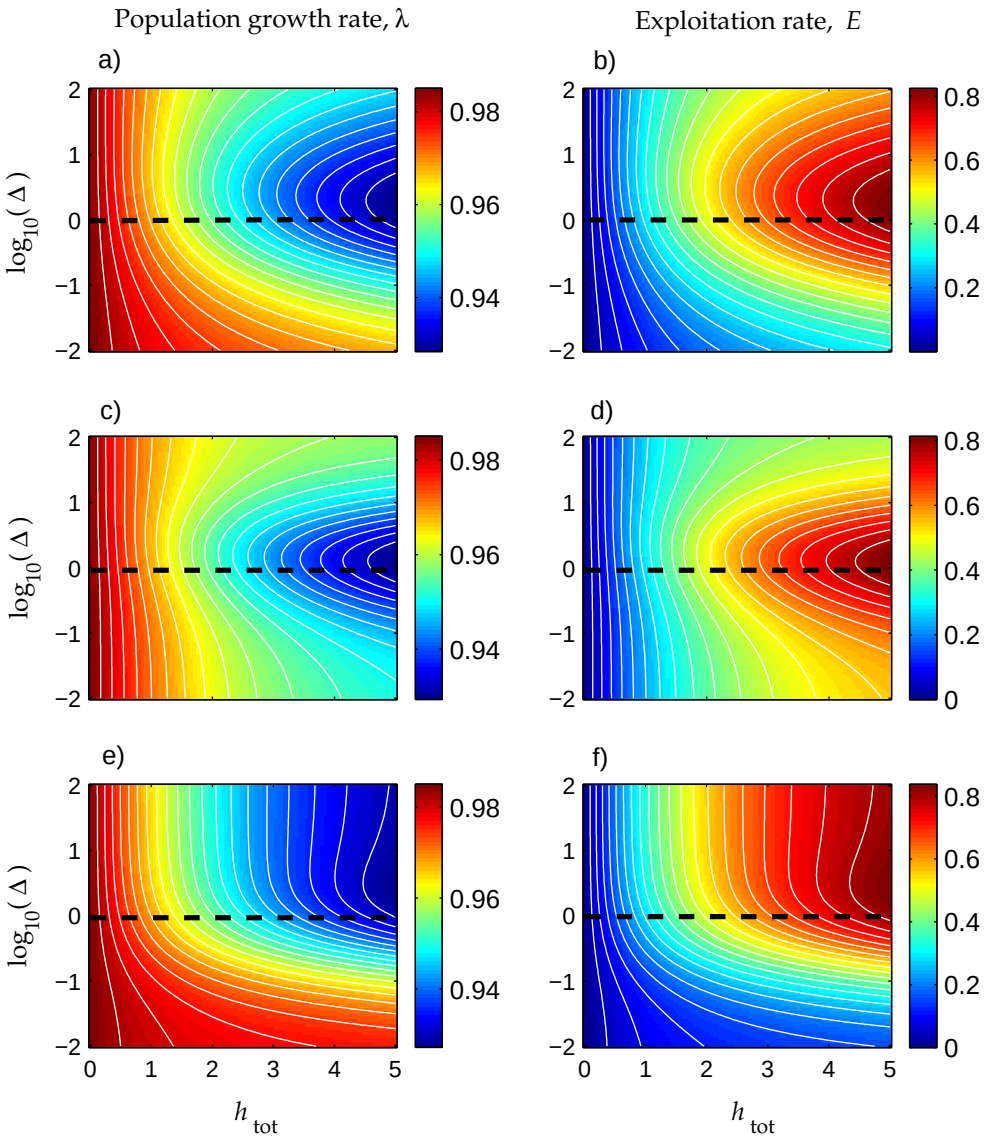
Figure 5 Elasticity of λ to demographic parameters, as a function of the total harvest intensity h_{tot}, with no selection. s_7 = breeder survival, s_6 = survival of $\geq$ third-year pre-breeders, w_{33} = transition of large chicks to large chicks, r_3 = survival of large relative to medium chciks, q_3 = proportion of large chicks produced, and $\bar{T}$ = mean duration of pre-breeder stage. See Table 2.)

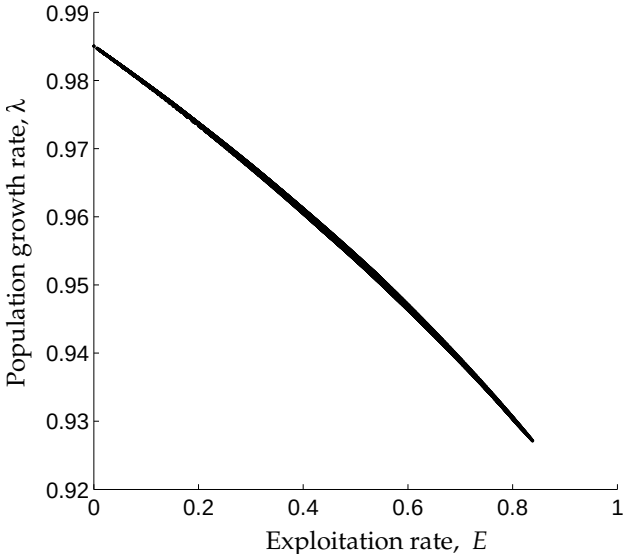
Figure 6 Effects of harvest intensity h_{tot} for the selectivity pattern estimated on Putauhinu Island. (a) λ as a function of h_{tot}, (b) E as a function of h_{tot}, (c) λ as a function of E.

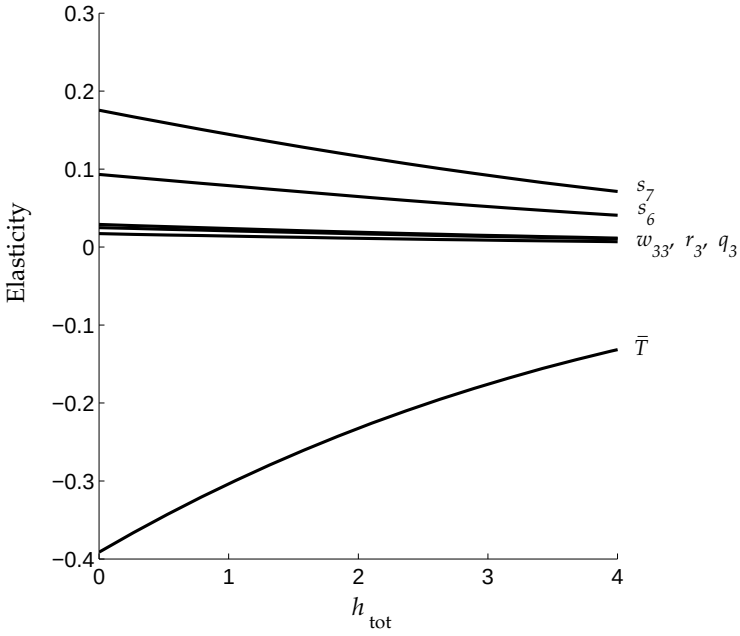
Figure 7 Reduction in λ resulting from combinations of chick and adult exploitation. White contours are isoclines of equal reduction in λ from 2 percentage points (lower left) to 20 percentage points (upper right). Note different scales on x and y axes.

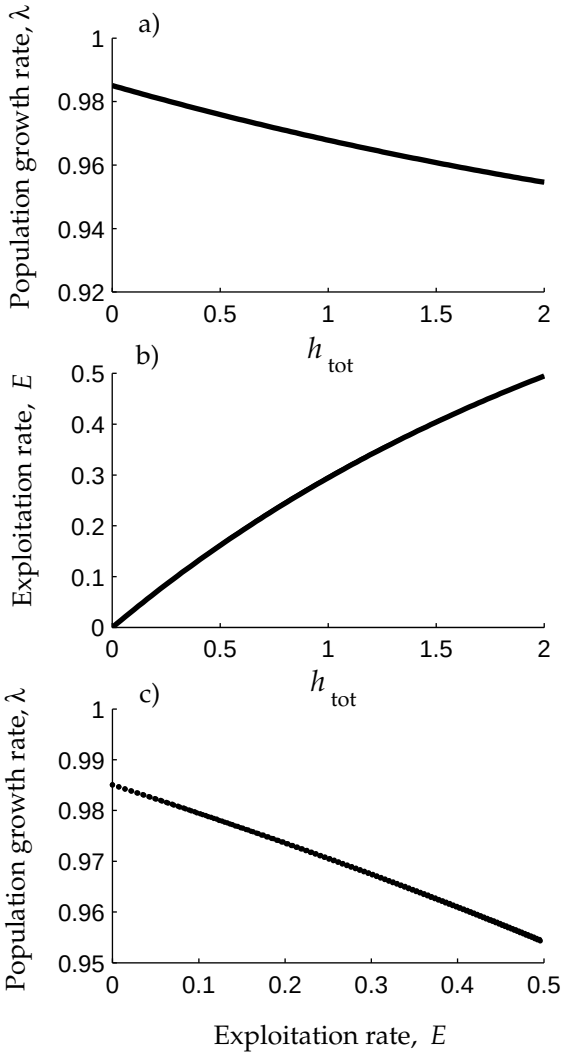

Chicks
Pre-breeders
Breeders
1
2
3
4
5
6
7
Nanao
(B)
Rama
(C)
Non-
harvest
(D)

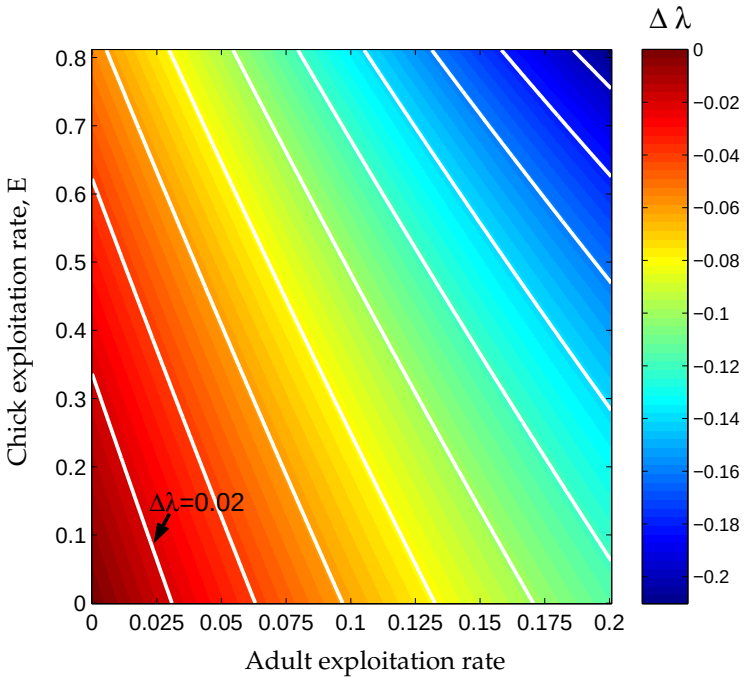

P[H]
h
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
1
2
3
4
5


Population growth rate, λ
Exploitation rate, E
a)
b)
c)
d)
e)
f)
log10(Δ)
h tot
0.98
0.96
0.94
0.8
0.6
0.4
0.2
0


0.99
0.98
0.97
0.96
0.95
0.94
0.93
0.92
Population growth rate, λ
0
0.2
0.4
0.6
0.8
1
Exploitation rate, E


0.3
0.2
0.1
0
−0.1
−0.2
−0.3
−0.4
0
1
2
3
4
Elasticity
h_{tot}
s_7
s_6
w_{33}, r_3, q_3
$\bar{T}$


a)
Population growth rate, λ
1
0.98
0.96
0.94
0.92
0
0.5
1
1.5
2
h tot
b)
Exploitation rate, E
0.5
0.4
0.3
0.2
0.1
0
0
0.5
1
1.5
2
h tot
c)
Population growth rate, λ
1
0.99
0.98
0.97
0.96
0.95
0
0.1
0.2
0.3
0.4
0.5
Exploitation rate, E


Δ λ
0
−0.02
−0.04
−0.06
−0.08
−0.1
−0.12
−0.14
−0.16
−0.18
−0.2
Chick exploitation rate, E
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Δλ=0.02
0
0.025
0.05
0.075
0.1
0.125
0.15
0.175
0.2
Adult exploitation rate